Journal of Insect Science OPEN ACCESS

RESEARCH

Temperature Effects on the Development and Reproduction of Three *Trichogramma* (Hymenoptera: Trichogrammatidae) Species Reared on *Trichoplusia ni* (Lepidoptera: Noctuidae) Eggs

F. S. Krechemer[1] and L. A. Foerster

Departamento de Zoologia, Universidade Federal do Paraná, P.O. Box 19.020 (81531-990), Curitiba, PR, Brazil
[1]Corresponding author, e-mail: flakrechemer@gmail.com

Subject Editor: Norman Leppla

J. Insect Sci. *(2015)* 15(1): 90; DOI: 10.1093/jisesa/iev072

ABSTRACT. The cabbage looper, *Trichoplusia ni* (Hübner) (Lepidoptera: Noctuidae) is a generalist species and an important pest of Brassicaceae worldwide. Egg parasitoids are a feasible alternative for the control of this species. We evaluated the suitability of *T. ni* eggs as hosts for three *Trichogramma* Westwood (Hymenoptera: Trichogrammatidae) species and their tolerance to survive and develop within a range of temperatures between 15 and 30°C under laboratory conditions. The species evaluated were *Trichogramma pretiosum* Riley, *Trichogramma atopovirilia* Oatman and Platner, and *Trichogramma acacioi* Brun, Moraes and Soares. Parasitism rate was affected by temperature, parasitoid species, and by the interaction between these two factors. Parasitoids developed and reproduced in the range of temperatures evaluated, but *Trichog. acacioi* failed to parasitize *T. ni* eggs at 30°C. The highest parasitism rates of *Trichog. atopovirilia* and *Trichog. pretiosum* occurred at 20 and 25°C and *Trichog. acacioi* at 25°C, with parasitism rate above 70% in the three species. Parasitoid emergence was not affected by temperature or species. The estimated thermal constant and lower temperature threshold were 134.6 DD and 10.6°C for *Trichog. pretiosum* and 130.1 DD and 11.2°C for *Trichog. atopovirilia*. The results demonstrated that *Trichog. pretiosum* and *Trichog. atopovirilia* are the most suitable species for the control of *T. ni*, as they can remain active throughout the year in subtropical regions.

Key Words: biological control, cabbage looper, crucifer, egg parasitoid, thermal requirement

The cabbage looper *Trichoplusia ni* (Hübner) (Lepidoptera: Noctuidae) is a generalist pest that feeds on more than 160 species of plants comprising 36 families (Sutherland and Green 1984). This species is an important pest of cucumber [*Cucumis sativus* (L.)], pepper [*Capsicum annuum* (L.)], tomato (*Solanum lycopersicon* Miller) (Sutherland and Green 1984), and one of the most important pests of brassicaceous crops, causing direct damage and significant yield losses (Maxwell et al. 2006). The excessive dependence on chemical insecticides affects natural enemies and promotes the selection of resistant strains of pests (Akhtar et al. 2007, 2010), in addition to causing environmental damage. Thus, biological control can be an alternative to the use of insecticides for controlling of *T. ni* (Milanez et al. 2009, Altoé et al. 2012).

The development of mass rearing and release techniques of parasitoids have promoted the use of *Trichogramma* Westwood (Hymenoptera: Trichogrammatidae) species (Jalali and Singh 1992, Jalali et al. 2007, Firake and Khan 2014). Inoculative biological control with *Trichogramma* species (van Lenteren and Bueno 2003, Cabello et al. 2012) has proven effective, especially in organic crops that are cultivated year-round such as brassicaceous crops, where the chance of establishment of natural enemies is higher in the absence of disruptive chemical insecticides (Zehnder et al. 2007). In this context, the ability of both host eggs and parasitoids to remain active throughout the year is an essential characteristic for a successful biological control program.

Currently, few species of *Trichogramma* have been reported parasitizing eggs of *T. ni*. Studies on the development of *Trichogramma pretiosum* Riley in eggs of *T. ni* and their use in biological control were carried out by Oatman and Platner (1971), Ashley et al. (1974), Butler and Lopez (1980) and recently by Milanez et al. (2009), and Altoé et al. (2012). However, these studies have not examined the effect of temperature on the development and reproduction of *Trichogramma*. In the 70 s and 80 s, studies were conducted on *Trichogramma platneri* Nagarkatti, *Trichogramma minutum* Riley, and *Trichogramma evanescens* Westwood in eggs of *T. ni* (Marston and Ertle 1973, Ashley et al. 1974, Parker and Pinnel 1974, Hohmann et al. 1988). However, these species do not occur in Brazil.

Other less studied species of *Trichogramma* may also have potential to control *T. ni*. *Trichogramma atopovirilia* Oatman and Platner and *Trichogramma acacioi* Brun, Moraes and Soares, as well as *Trichog. pretiosum*, are naturally found in Southern Brazil and were collected parasitizing eggs of the velvetbean caterpillar *Anticarsia gemmatalis* Hübner in soybean fields, during summer, in Southeastern Paraná State (Avanci et al. 2005, Foerster and Foerster 2009). Milanez et al. (2009) compared the development and reproduction of six species of *Trichogramma,* including *Trichog. acacioi* and *Trichog. atopovirilia* in *T. ni* eggs, at 25°C. However, subtropical mean temperatures in Southern Brazil range from 13 to 15°C in winter (with periods with temperatures near 0°C), to 22°C in summer (sometimes exceeding the range of 25°C) (Foerster and Foerster 2009), exposing *Trichogramma* species to a wider range of temperature than in tropical areas. Therefore, naturally occurring species in subtropical region tend to be more successful as biological control agents in this temperature regime, since they are adapted to a wider range of temperature. Under such conditions, the biological characteristics of parasitoids and their interactions with their host will determine the suitability of the species to effectively control the target host (Bourchier and Smith 1996).

Brassicaceous crops are grown year-round in subtropical areas of Brazil and elsewhere, exposing both pests and their natural enemies to a wide range of temperatures. For two species, *Trichog. atopovirilia* and *Trichog. acacioi*, there are no data available on the effect of temperatures as low as 15°C on the development and reproduction of these species on eggs of *T. ni*. *Trichog. pretiosum* is a widely studied species on many hosts; however, the host egg, as well as its nutritional characteristics are known to alter the thermal requirements and biological characteristics of the parasitoid (Bueno et al. 2009). For this reason, *Trichog.*

pretiosum was included as a reference for comparison with the two other species.

We evaluate the development of different species of *Trichogramma* in the temperature range between 15°C and 30°C to select the most suitable species to be used for the control of *T. ni*. The estimated lower temperature threshold was used to evaluate the ability of the parasitoid in remaining active throughout the year. We used this information as an additional criteria for the selection of species, considering that brassicas are cultivated throughout the year in Brazil, and the parasitoid should be effective during this period.

Materials and Methods

Origin and Rearing Procedures of *T. ni* and *Trichogramma* Species. A colony of *T. ni* was established in 2008 with larvae and pupae collected from commercial crops of broccoli and cauliflower located in Colombo (25° 17′ 31″ S, 49° 13′ 26″ W), Southeastern Paraná State, Southern Brazil. Approximately 30 newly hatched caterpillars were kept per Petri dish (18 by 1 cm) containing a disk of absorbent paper and leaves of broccoli. This initial number of caterpillars in the dishes was reduced as they increased in size. Pupae were maintained in plastic containers (12 by 5 cm) until adult emergence. Adults were fed a 10% honey solution soaked in a cotton ball in a Petri dish. This concentration has been shown to increase fertility and longevity for adults (Binder 1996, Tisdale and Sappington 2001, Marchioro and Foerster 2012) and is commonly used as food for noctuid adults. Adults were maintained in glass cages (45 by 33 by 35 cm) at ambient temperature (18–22°C), with the inner sides covered with acrylic plates and openings for ventilation and maintenance. An excised leaf of broccoli or cauliflower was provided to stimulate egg laying and as a substrate for oviposition. The eggs laid on the leaves were removed with a fine brush, and those laid on the acrylic plates were washed and then collected using a strainer with fine mesh. All eggs were transferred to Petri dishes (15 by 1 cm) lined with paper towel and placed in a chamber at 20 ± 1°C and RH 70 ± 10%.

The colonies of *Trichog. pretiosum, Trichog. atopovirilia,* and *Trichog. acacioi* were established in the laboratory with parasitized eggs of *A. gemmatalis* collected from soybean crops in Southeastern Paraná State, Southern Brazil. The species were reared on eggs of the wheat armyworm *Pseudaletia sequax* Franclemont for 15 generations. Subsequently, the parasitoids were maintained for three generations in *T. ni* eggs before of the experiments. The rearing methods followed Foerster and Foerster (2009).

Temperature Effects on Parasitoids. The experiments were conducted in climatic chambers at constant temperatures of 15, 20, 25, and 30 ± 1°C, photoperiod of 12:12 (L:D) h, and 70 ± 10% RH. Paper cartons (0.5 by 1.5 cm) containing 20 eggs of *T. ni* less than 24 h old were exposed to ultraviolet light for 30 min for sterilization. Newly emerged female parasitoids were kept in the presence of males to mate for 24 h. After this period, females were maintained individually in 0.5 by 6 cm glass tubes sealed with a piece of cotton and presented with 20 eggs of *T. ni* for 24 h, at each temperature evaluated. After this period, females were removed and the eggs placed inside the tubes and maintained in the climatic chambers. The eggs were monitored daily to check the development of the parasitoids, indicated by the blackening of the eggs (Knutson 1998). After the majority of parasitoids emerged, the remaining eggs were kept for three additional days to ensure that any delayed emergence was recorded. Twenty replicates were performed for each temperature. All emerged adults were fed daily with honey and their longevity and sex ratio were recorded.

Thermal Requirements. The lower temperature threshold (L_0) and thermal constant (K) were estimated for *Trichog. pretiosum* and *Trichog. atopovirilia*. The development rate (1/development days) was regressed against temperature using the linear regression equation ($Y = a + bx$). The lower temperature threshold was calculated with the x-intercept method ($T_0 = -a/b$), and the thermal constant by the reciprocal of the slopes of the estimated regression lines ($K = 1/b$) (Campbell et al. 1974). The linear regression requires a minimum of four points to accurately estimate the parameters (Haddad et al. 1999), thus the thermal requirements of *Trichog. acacioi* were not estimated, because this species did not parasitize at 30°C. Additionally, survival in different temperature regimes was compared using survival curves constructed according to the Kaplan–Meier function (Kaplan and Meier 1958).

Statistical Analysis. The normality of the data and the homogeneity of the variance were assessed with the Shapiro–Wilk's test and Levene's test, respectively. The data on parasitism, emergence, sex ratio, and longevity were not normally distributed and were transformed to log ($x + 1$). The transformed data were compared using a factorial analysis of variance (ANOVA) with parasitoid species and temperature as sources of variation (3 by 4). When significant, the means were compared with the Tukey's test ($P < 0.05$). All statistical procedures were performed using the software Statistica v.7 (Statsoft 2004).

Results

Parasitism and Development Time. The percentage of parasitism was significantly influenced by temperature ($F = 50.56$; $F_{(2,203)}$; $P < 0.05$), species ($F_{(1,203)} = 7.37$; $P = 0.01$) and by the interaction between these two factors ($F_{(5,203)} = 2.39$; $P < 0.05$). The percentage of *T. ni* eggs parasitized by *Trichog. atopovirilia* was significantly higher than that of *Trichog. acacioi* in all temperatures evaluated and also higher than that of *Trichog. pretiosum*, although statistically significant only at 15° and 25°C. Parasitism rate of *Trichog. pretiosum* was similar between 20 and 30°C but lower at 15°C (Table 1). For *Trichog. atopovirilia*, both upper and lower temperatures resulted in significantly lower parasitism rates than at 20 and 25°C. At 30°C, *Trichog. acacioi* failed to parasitize eggs of *T. ni*, whereas at 25°C, the percentage of parasitized eggs was significantly higher than at 15 or 20°C (Table 1).

The development time of parasitoids was influenced by temperature ($F_{(2,175)} = 66830.18$; $P < 0.05$), parasitoid species ($F_{(1,\ 175)} = 254.04$; $P < 0.05$), and the interaction between these factors ($F_{(5,175)} = 233.44$; $P < 0.05$). Development time of the three parasitoid species decreased as temperature increased (Table 1).

Emergence, Sex Ratio, Longevity, and Survival. The percentage of emergence and sex ratio were not affected by temperature, parasitoid species, or by the interaction between the two factors ($F_{(4,174)} = 0.44$; $P = 0.78$; $F_{(4,169)} = 0.65$; $P = 0.63$, respectively) (Table 2).

Longevity of males and females was affected by temperature ($F_{(2,158)} = 37.95$; $P < 0.05$; $F_{(2,153)} = 105.99$; $P < 0.05$, respectively) and by the interaction between temperature and species ($F_{(5,158)} = 3.32$; $P < 0.05$; $F_{(5,153)} = 4.65$; $P < 0.05$, respectively). Longevity was inversely proportional to temperature for both males and females, but the life span of females of *Trichog. pretiosum* and females and males of *Trichog. atopovirilia* at 20°C was shorter than those at 25°C. No differences in longevity were found between *Trichog. atopovirilia* and *Trichog. pretiosum* in all temperatures, except at 30°C, when males and females of *Trichog. atopovirilia* lived significantly longer than *Trichog. pretiosum*. Longevity of both sexes of *Trichog. acacioi* was significantly lower than *Trichog. pretiosum* and *Trichog. atopovirilia*, except at 20°C, where the life span of males and females was similar to the two other species (Table 2).

The Kaplan–Meier analysis showed that the survival rates of females of *Trichog. pretiosum* ($\chi^2_{(3)} = 431.71$; $P < 0.05$), *Trichog. atopovirilia* ($\chi^2_{(3)} = 847.67$; $P < 0.05$), and *Trichog. acacioi* ($\chi^2_{(2)} = 262.70$; $P < 0.05$) were affected by temperature. Differences in survival among the three species were observed at 15°C ($\chi^2_{(2)} = 105.65$; $P < 0.05$), 20°C ($\chi^2_{(2)} = 59.01$; $P < 0.05$), and 25°C ($\chi^2_{(2)} = 438.69$; $P < 0.05$) and between *Trichog. pretiosum* and *Trichog. atopovirilia* at 30°C (log-rank test = 11.03; $P < 0.05$) (Fig. 1).

Thermal Requirements. The linear regression equation described the relationship between development rate of *Trichog. pretiosum* and

Table 1. Mean (±SE) percentage of parasitism and developmental time of *Trichog. pretiosum*, *Trichog. atopovirilia,* and *Trichog. acacioi* reared on eggs of *T. ni* at different temperatures

Parameter	Temperature (°C)	*Trichog. pretiosum*	*Trichog. atopovirilia*	*Trichog. acacioi*
Parasitism (%)[a]	15	19.1 ± 2.8 bB	46.3 ± 7.6 cA	25.5 ± 4.2 bB
	20	70.5 ± 7.6 aA	74.0 ± 8.2 abA	42.1 ± 6.9 bB
	25	72.8 ± 6.1 aB	90.3 ± 1.2 aA	74.1 ± 7.2 aB
	30	59.1 ± 6.2 aA	60.0 ± 8.1 bcA	—[b]
Developmental time[a]	15	28.8 ± 0.1 aB	32.5 ± 0.2 aA	28.6 ± 0.1 aB
	20	15.6 ± 0.1 bB	15.9 ± 0.1 bAB	16.0 ± 0.0 bA
	25	9.0 ± 0.0 cB	9.0 ± 0.0 cB	10.0 ± 0.0 cA
	30	7.0 ± 0.0 dA	7.0 ± 0.0 dA	—[b]

[a]Means followed by the same lowercase letter (columns) and means followed by same uppercase letter (rows) do not differ significantly by Tukey test ($P < 0.05$).
[b]Parameter not assessed due to absence of parasitism.

Table 2. Mean (±SE) emergence percentage, sex ratio, and longevity (days) of females and males of *Trichog. pretiosum*, *Trichog. atopovirilia,* and *Trichog. acacioi* reared on eggs of *T. ni* at different temperatures

Parameter	Temperature (°C)	*Trichog. pretiosum*	*Trichog. atopovirilia*	*Trichog. acacioi*
Emergence (%)[a]	15	84.4 ± 6.6 aA	96.5 ± 1.7 aA	95.0 ± 3.1 aA
	20	83.1 ± 8.5 aA	95.9 ± 3.6 aA	85.8 ± 5.7 aA
	25	99.5 ± 0.4 aA	98.7 ± 1.3 aA	98.5 ± 1.1 aA
	30	79.5 ± 7.5 aA	82.1 ± 8.3 aA	—[b]
Sex ratio[a]	15	0.66 ± 0.07 aA	0.85 ± 0.02 aA	0.60 ± 0.06 aA
	20	0.59 ± 0.09 aA	0.77 ± 0.07 aA	0.54 ± 0.08 aA
	25	0.75 ± 0.05 aA	0.81 ± 0.03 aA	0.73 ± 0.07 aA
	30	0.68 ± 0.06 aA	0.82 ± 0.03 aA	—[b]
Longevity ♀[a]	15	19.7 ± 1.2 aA	22.2 ± 0.6 aA	16.3 ± 0.6 aB
	20	9.5 ± 1.4 bA	8.2 ± 1.9 cA	9.4 ± 1.0 bA
	25	12.1 ± 0.9 bA	13.6 ± 0.7 bA	6.2 ± 0.2 cB
	30	2.3 ± 0.2 cB	4.4 ± 0.5 cA	—[b]
Longevity ♂[a]	15	15.7 ± 1.1 aA	16.6 ± 0.9 aA	12.1 ± 0.8 aB
	20	10.1 ± 1.8 bA	7.3 ± 1.7 cA	9.3 ± 0.8 bA
	25	9.6 ± 0.7 bA	11.2 ± 0.7 bA	6.5 ± 0.2 cB
	30	2.3 ± 0.2 cB	4.4 ± 0.5 cA	—[b]

[a]Means followed by the same lowercase letter (columns) and means followed by same uppercase letter (rows) do not differ significantly by Tukey test ($P < 0.05$).
[b]Parameter not assessed due to absence of parasitism.

Trichog. atopovirilia and temperature, as indicated by the coefficient of determination of 0.99 for both species (Fig. 2). The values of T_0 were 10.6 (±0.09) and 11.2 (±0.08)°C for *Trichog. pretiosum* and *Trichog. atopovirilia*, respectively. The estimated thermal constants were 137.6 (±8.55) DD for *Trichog. pretiosum* and 130.1 (±7.72) DD for *Trichog. atopovirilia* (Fig. 2). The thermal requirements of *Trichog. acacioi* were not estimated, as this species did not parasitize eggs of *T. ni* at 30°C.

Discussion

Temperature affects immature development, adult emergence, reproduction, and longevity of insects, since they are constantly exposed to temperature fluctuations in their natural environment and may show differences in tolerance to extreme temperatures and in their acclimation responses (Lessard and Boivin 2013, Firake and Khan 2014). The number of eggs parasitized by a female of *Trichogramma* is a determining factor in the choice of a species or strain to be used in a biological control program (Kalyebi et al. 2005). This study recorded that the three investigated species parasitized at 15°C, besides, parasitism rates above 70% were recorded at temperatures of 20 and 25°C for *Trichog. atopovirilia* and *Trichog. pretiosum*, and at 25°C for *Trichog. acacioi*. Although, in some cases differences were not statistically significant, *Trichog. atopovirilia* tended to have higher rates of parasitism throughout the range of temperatures evaluated. Milanez et al. (2009) evaluated the suitability of *T. ni* eggs as hosts for four *Trichogramma* species at 25°C. The eggs of *T. ni* were accepted by all species, but the percentage of parasitism was lower than those reported in our study. This might have occurred because the parasitoids used in their experiment were previously reared on the small eggs of *Anagasta kuehniella* (Zeller, 1879). Previous studies concluded that larger eggs with higher nutritional content generate larger females, with higher parasitism capacity and longevity (Kazmer and Luck 1995, Doyon and Boivin 2005). Therefore, the more vigorous parasitoids obtained from large eggs of *P. sequax,* and posteriorly *T. ni*, used in our experiment, might explain the better performance of the *Trichogramma* species.

According to Pak and van Lenteren (1988), species and strains with good performance in the laboratory are more likely to have a better performance in the field. In this study, with the exception of *Trichog. acacioi,* which did not parasitize at 30°C, the emergence of the three parasitoid species was not affected by the temperatures tested. The rates of parasitism and emergence of *Trichog. pretiosum* and *Trichog. atopovirilia* at all examined temperatures indicate that these species have a high potential to control *T. ni* in brassicaceous crops year round. *Trichog. acacioi* proved to be effective in temperatures below 30°C, thus becoming a good option for biological control except during summer months. In brassicaceous crops, because of their continuous cultivation, hosts are also available in the field throughout the year. Even in periods when *T. ni* is not available on the field, parasitoids may use other lepidopteran pests of *Brassicae* as hosts, such as *Plutella xylostella* (L.) and *Spodoptera eridania* (Cramer) (Pratissoli et al. 2008, Goulart et al. 2011, Goulart et al. 2012). Thus, the thermal tolerance of the tested species in this study, to both winter and summer temperatures

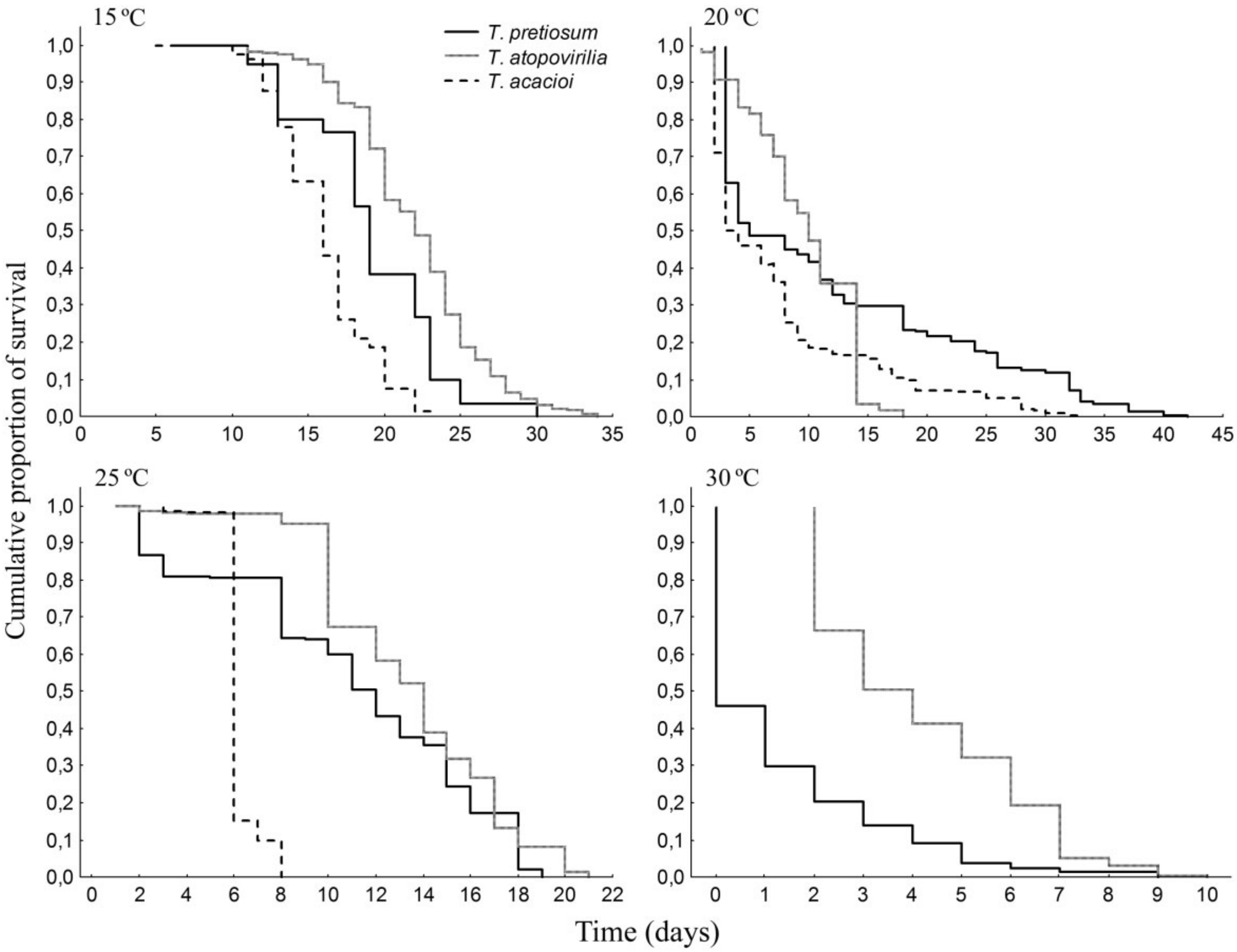

Fig. 1. Female survival curve of *Trichog. pretiosum*, *Trichog. atopovirilia*, and *Trichog. acacioi* reared on eggs of *T. ni* at constant temperatures of 15, 20, 25, and 30°C.

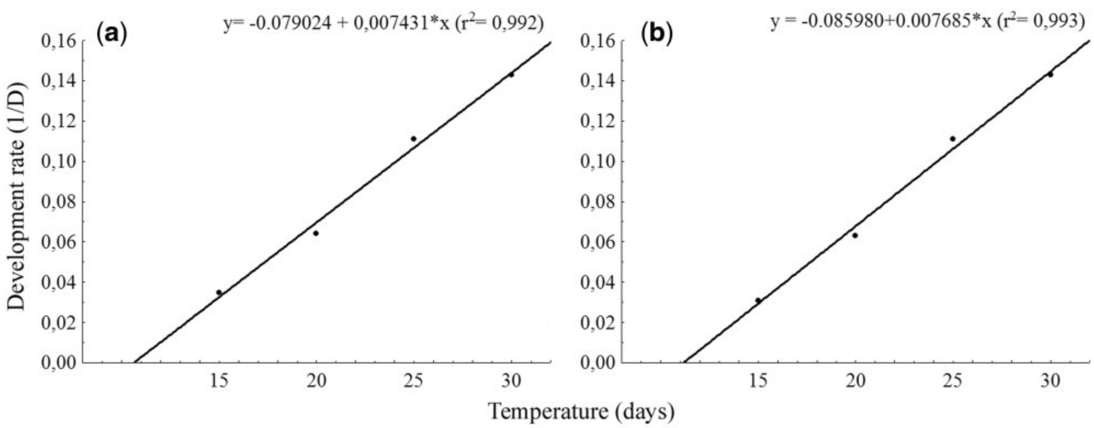

Fig. 2. Linear regression equation of the development rate (1/*D*) of *Trichog. pretiosum* (a) and *Trichog. atopovirilia* (b) reared on eggs of *T. ni.*

in Southern Brazil, along with a constant availability of hosts in the field make these species suitable candidates as biocontrol agents of *T. ni* in subtropical regions.

The development time of all species increased as temperature decreased, as previously described for other *Trichogramma* species (Haile et al. 2002, Bueno et al. 2009, Altoé et al. 2012, Lessard and Boivin 2013). The nutritional requirements of insects and their body mass have been reported as important factors affecting the thermal constant (K) and base temperature (T_0) (Haddad et al. 1999, Charnov and Gilloby 2003). The base temperature (T_0) of *Trichog. pretiosum* (10.6°C) and *Trichog. atopovirilia* (11.2°C) were below average winter temperatures in Southern Brazil (13–15°C). *Trichogramma* species show different strategies to survive during winter, which varies depending on the host, individual characteristics of the species, and its geographic origin (Boivin 1994). Some species are able to stay active using alternative hosts (Babendreier et al. 2003, Özder and Saglam 2005), while others enter a state of quiescence or diapause under unfavourable environmental conditions (Curl and Burbutis 1977, Garcia et al. 2002, Rundle and Hoffmann 2003). It was not possible to estimate the lower threshold temperature of *Trichog. acacioi* in this study; however, Foerster et al. (2015) reported that *Trichog. acacioi* and *Trichog. pretiosum* are able to remain active during winter in Southern Brazil.

In conclusion, based on parasitism and emergency rates, as well as the estimated base temperature, *Trichog. pretiosum* and *Trichog. atopovirilia* are the most suitable species for the control of *T. ni*, since they can remain active throughout the year in subtropical regions.

Acknowledgments

The authors thank the Brazilian National Research Council (CNPq) for scholarship and financial support.

References Cited

Akhtar, Y., M. B. Isman, P. M. Paduraru, S. Nagabandi, R. Nair, and E. Plettner. 2007. Screening of dialkoxybenzenes and disubstituted cyclopentene derivatives against the cabbage looper, *Trichoplusia ni*, for the discovery of new feeding and oviposition deterrents. J. Agric. Food. Chem. 55: 10323–10330.

Akhtar, Y., Y. Yu, M. B. Isman, and E. Plettner. 2010. Dialkoxybenzene and dialkoxyallylbenzene feeding and oviposition deterrents against the cabbage looper, *Trichoplusia ni*: potential insect behavior control agents. J. Agric. Food. Chem. 58: 4983–4991.

Altoé, T. S., D. Pratissoli, J. R. Carvalho, H.J.G. Santos Junior, J.P.P. Paes, R.C.O.F. Bueno, and A. F. Bueno. 2012. *Trichogramma pretiosum* (Hymenoptera: Trichogrammatidae) parasitism of *Trichoplusia ni* (Lepidoptera: Noctuidae) eggs under different temperatures. Ann. Entomol. Soc. Am. 105: 82–89.

Ashley, T. R., J. C. Allen, and D. Gonzalez. 1974. Successful parasitization of *Heliothis zea* and *Trichoplusia ni* eggs by *Trichogramma*. Environ. Entomol. 3: 319–322.

Avanci, M.R.F., L. A. Foerster, and C. L. Cañete. 2005. Natural parasitism in eggs of *Anticarsia gemmatalis* Hübner (Lepidoptera: Noctuidae) by *Trichogramma* spp. (Hymenoptera: Trichogrammatidae) in Brazil. Rev. Bras. Entomol. 49: 148–151.

Babendreier, D., S. Kuske, and F. Bigler. 2003. Overwintering of the egg parasitoid *Trichogramma brassicae* in Northern Switzerland. Biocontrol 48: 261–273.

Binder, B. F. 1996. Effect of carbohydrate on age-related feeding behaviors and longevity in adult black cutworm, *Agrotis ipsilon* (Lepidoptera: Noctuidae). J. Insect. Behav. 9: 215–222.

Boivin, G. 1994. Overwintering strategies of egg parasitoids, pp. 219–244. *In* A. Wajnberg and S. A. Hassan (eds.), Biological control with egg parasitoids. CAB International, Wallingford, UK.

Bourchier, R. S., and S. M. Smith. 1996. The effect of host size on quality attributes of the egg parasitoid *Trichogramma pretiosum*) Influence of environmental conditions and parasitoid quality on field performance of *Trichogramma minutum*. Entomo. Exp. Appl. 80: 461–468.

Bueno, R.C.O. F., J.R.P. Parra, A. F. Bueno. 2009. Biological characteristics and thermal requirements of a Brazilian strain of the parasitoid *Trichogramma pretiosum* reared on eggs of *Pseudoplusia includens* and *Anticarsia gemmatalis*. Biol. Control 51: 355–361.

Butler, G. D., and J. D. Lopez. 1980. *Trichogramma pretiosum*. Development in two hosts in relation to constant and fluctuating temperatures. Ann. Entomol. Soc. Am. 73: 671–673.

Cabello, T., J. R. Gallego, F. J. Fernandez, M. Gamez, E. Vila, M. del Pino, and E. Hernandez Suarez. 2012. Biological control strategies for the South American tomato moth (Lepidoptera: Gelechiidae) in greenhouse tomatoes. J. Econ. Entomol. 105: 2085–2096.

Campbell, A., B. D. Frazer, A. P. Gutierrez, and A. P. Macknauer. 1974. Temperature requirements of some aphids and their parasites. J. Appl. Ecol. 11: 431–438.

Charnov, E. L., and J. F. Gilloby. 2003. Thermal time: body size, food quality and the 10°C rule. Evol. Ecol. Res. 5: 43–51.

Curl, G. D., and P. P. Burbutis. 1977. The mode of overwintering of *Trichogramma nubilale* Ertle and Davis. Environ. Entomol. 6: 629–636.

Doyon, J., and G. Boivin. 2005. The effect of development time on the fitness of female *Trichogramma evanescens*. J. Insect. Sci. 5: 1–5.

Firake, D. M., and M. A. Khan. 2014. Alternating temperatures affect the performance of *Trichogramma* species. J. Insect. Sci. 14: 41.

Foerster, M. R., and L. A. Foerster. 2009. Effects of temperature on the immature development and emergence of five species of *Trichogramma*. BioControl 54: 445–450.

Foerster, M. R., C. A. Marchioro, and L. A. Foerster. 2015. How *Trichogramma* survives during soybean offseason in Southern Brazil and the implications for its success as a biocontrol agent. BioControl 60: 1–11.

Garcia, P. V., E. Wajnberg, J. Pizzol, and M.L.M. Oliveira. 2002. Diapause in the egg parasitoid *Trichogramma cordubensis*: role of temperature. J. Insect. Physiol. 48: 349–355.

Goulart, M.M.P., A. F. Bueno, R.C.O.F. Bueno, and S. S. Vieira. 2011. Interaction between *Telenomus remus* and *Trichogramma pretiosum* in the management of *Spodoptera* spp. Rev. Bras. Entomol. 55: 121–124.

Goulart, R. M., H.X.L. Volpe, A. M. Vacari, R. T. Thuler, and S. A. Bortoli. 2012. Insecticide selectivity to two species of *Trichogramma* in three different hosts, as determined by IOBC/WPRS methodology. Pest. Manage. Sci. 68: 240–244.

Haddad, M. L., J.R.P. Parra, and R.C.B. Moraes. 1999. Métodos para estimar os limites térmicos inferior e superior de desenvolvimento de insetos. FEALQ, Piracicaba, São Paulo, Brazil.

Haile, A. T., S. A. Hassan, C.K.P.O. Ogol, J. Baumgärtner, S. Sithanantham, J. C. Monje, and C.P.W. Zebits. 2002. Temperature-dependent development of four egg parasitoids *Trichogramma* species (Hymenoptera; Trichogrammatidae). Biocontrol Sci. Technol. 12: 555–567.

Hohmann, C. L., R. F. Luck, and E. R. Oatman. 1988. A comparision of longevity and fecundity of adult *Trichogramma platneri* (Hymenoptera: Trichogrammatidae) reared from eggs of the cabbage looper and the grain moth, with and without access to honey. J. Econ. Entomol. 81: 1307–1312.

Jalali, S. K., and S. P. Singh. 1992. Differential response of four *Trichogramma* species to low temperatures for short term storage. Entomophaga 37: 159–165.

Jalali, S. K., T. Venkatesan, K. S. Murthy, R. J. Rabindra, and Y. Lalitha. 2007. Vacuum packaging of *Corcyra cephalonica* (Staiton) eggs to enhance shelf life for parasitization by the egg parasitoid *Trichogramma chilonis*. Biol. Control 41: 64–67.

Kalyebi, A., W. A. Overholt, F. Schulthess, J. M. Mueke, S. A. Hassan, and S. Sithanantham. 2005. Functional response of six indigenous trichogrammatid egg parasitoids (Hymenoptera: Trichogrammatidae) in Kenya: influence of temperature and relative humidity. Biol. Control 32: 164–171.

Kaplan, E. L., and P. Meier. 1958. Nonparametric estimation from incomplete observations. J. Am. Stat. Assoc. 53: 457–481.

Kazmer, D. J., and R. F. Luck. 1995. Field tests of size-fitness hypothesis in the egg parasitoid *Trichogramma pretiosum*. Ecology 76: 412–425.

Knutson, A. 1998. The *Trichogramma* manual. Texas Agriculture Extension Service, Texas A&M University System, College Station, TX.

Lessard, E., and G. Boivin. 2013. Effect of low temperature on emergence, fecundity, longevity and host-feeding by *Trichogramma brassicae*. BioControl 58: 319–329.

Marchioro, C. A., and L. A. Foerster. 2012. Importance of carbohydrate sources to the reproductive output of the wheat armyworm *Pseudaletia sequax*. Agric. For. Entomol. 14: 29–35.

Marston, N., and L. R. Ertle. 1973. Host influence on the bionomics of *Trichogramma minutum*. Ann. Entomol. Soc. Am. 66: 1155–1162.

Maxwell, E. M., H. Y. Fadamiro, and J. R. McLaughlin. 2006. Suppression of *Plutella xylostella* and *Trichoplusia ni* in cole crops with attracticide formulations. J. Econ. Entomol. 99: 1334–1344.

Milanez, A. M., D. Pratissoli, R. A. Polanczyk, A. F. Bueno, and C.B.A. Tufik. 2009. Avaliação de *Trichogramma* spp. para controle de *Trichoplusia ni*. Pesq. Agropec. Bras. 44: 1219–1224.

Oatman, E. R., and G. R. Platner. 1971. Biological control of the tomato fruitworm, cabbage looper, and hornworms on processing tomatoes in southern California, using mass releases of *Trichogramma pretiosum*. J. Econ. Entomol. 64: 501–506.

Özder, N., and O. Saglam. 2005. Overwintering of the egg parasitoids *Trichogramma brassicae* and *T. cacoeciae* (Hymenoptera: Trichogrammatidae) in the Thrace region of Turkey. J. Pest. Sci. 78: 129–132.

Pak, G. A., and J. C. van Lenteren. 1988. Criteria and methods for the prerelease evaluation of different *Trichogramma* spp. Strains, pp. 433–442. *In* J. Voegele, J. Waage, and J. C. van Lenteren (eds.), *Trichogramma* and other egg parasitoids, Proceedings of 2nd International Symposium on *Trichogramma*, Publication 43. Les colloques de I'INRA, Paris.

Parker, F. D., and R. E. Pinnel. 1974. Effectiveness of *Trichogramma* spp. in parasitizing eggs of *Pieris rapae* and *Trichoplusia ni* in the laboratory. Environ. Entomol. 3: 935–938.

Pratissoli, D., R. A. Polanczyk, A. M. Holtz, L. P. Dalvi, A. F. Silva, and L. N. Silva. 2008. Selection of *Trichogramma* species for controlling the Diamondback moth. Hortic. Bras. 26: 259–261.

Rundle, B. J., and A. A. Hoffmann. 2003. Overwintering of *Trichogramma funiculatum* Carver (Hymenoptera: Trichogrammatidae) under semi-natural conditions. Environ. Entomol. 32: 290–298.

Statsoft Inc. 2004. Software Statistica 7. EUA, Tulsa, EUA.

Sutherland, D.W.S., and G. L. Green. 1984. Cultivated and wild host plants. Suppression and management of cabbage looper populations. Technical Bulletin No. 1684. United States Department of Agriculture, Columbia, EUA.

Tisdale, R. A., and T. W. Sappington. 2001. Realized and potential fecundity, egg fertility, and longevity of laboratory-reared female beet armyworm (Lepidoptera: Noctuidae) under different adult diet regimes. Ann. Entomol. Soc. Am. 94: 415–419.

van Lenteren, J. C., and V.H.P. Bueno. 2003. Augmentative biological control of arthropods in Latin America. BioControl 48: 123–139.

Zehnder, G., G. M. Gurr, S. Kühne, M. R. Wade, S. D. Wratten, and E. Wyss. 2007. Arthropod pest management in organic crops. Annu. Rev. Entomol. 52: 57–80.

Received 18 March 2015; accepted 12 June 2015.